A NEW FRESHWATER LIMULOID FROM THE MIDDLE TRIASSIC OF NEW SOUTH WALES

by J. W. PICKETT

ABSTRACT. *Dubbolimulus peetae* gen. et sp. nov. is described from freshwater strata of middle Triassic age near Dubbo, New South Wales, and is referred to the new family Dubbolimulidae. Previous reports of xiphosurans from Australia are reviewed; *Pincombella belmontensis* Chapman, 1932 and *Hemiaspis tunnecliffei* Chapman, 1932 are shown to be respectively an insect and a trilobite.

REPORTS of merostomes from Australia are contained in only eight publications. Three of these (McCoy 1899; Gill 1951; Caster and Kjellesvig-Waering 1953) deal with eurypterids, and are not further mentioned in this article. A fourth (Quilty 1972) reports an unnamed Cambrian aglaspid from Tasmania. The remaining four (Chapman 1932; Riek 1955, 1968*b*; Riek and Gill 1971) are concerned with xiphosurans, and are summarized briefly.

AUSTRALIAN XIPHOSURANS

Chapman (1932) established the taxa *P. belmontensis* from the insect beds (?Boolaroo Sub-group, late Permian) near Belmont, New South Wales, and *H. tunnecliffei* from the late Silurian Dargile Formation at Studley Park, Kew, Victoria. Much better preserved than either of these is the magnificent specimen of the rather anomalous *Austrolimulus fletcheri* from the Beacon Hill shale lens in the middle Triassic Hawkesbury Sandstone of the Sydney district (Riek 1955, 1968*b*). The youngest xiphosuran so far known from the Australian continent is *Victalimulus mcqueeni* Riek and Gill, 1971 from the early Cretaceous fish bed (Strzelecki Group) near Koonwarra in Victoria (Waldman 1971).

Three of these papers are based on careful examination of available material. On the other hand, neither of the two species described by Chapman (1932) is xiphosuran. The holotype specimen of *P. belmontensis* (Pl. 56, fig. 2) is clearly the wingless and, for the most part, legless body of a hemipteran with a small scutellum and distinct pronotal lobes. Riek (1968*a*) lists sixty-two species of Hemiptera from the horizon yielding *P. belmontensis*. These are based on generally incomplete animals, either wings, heads, or thoraxes; since so few are known in all aspects of their morphology, no attempt is made here to reconcile *P. belmontensis* with any of the described forms. Chapman's figures (1932, pl. 14, figs. 1–3) are difficult to interpret in relation to the specimen. He appears to have taken some irregularity in the matrix to be the anterior border of his figs. 2 and 3 ('Anterior border . . . marked out by a definite rust-stained impression') and the real anterior margin to mark the edge of 'opercular plates'. Chapman considered that he was examining the specimen in ventral aspect, whereas it represents the back of the insect from which the wings have been torn. This, together with its distorted position, may have led him to interpret the only preserved, jointed leg as a dorsally attached telson. Chapman's fig. 2 was reproduced by Størmer (1955, fig. 13.6), who, for reasons now apparent, could not place *Pincombella* within any of the defined subdivisions of the suborder Limulina, listing it (p. P23) under 'Superfamily and Family uncertain'. For similar reasons it was referred to 'incertae sedis' by Bergström (1975).

The true affinities of the other species described by Chapman, *H. tunnecliffei*, are not immediately so clear. It is certain that Chapman's reconstruction (1932, pl. 14, fig. 5) bears no resemblance to the actual specimen. The broad anterior border with radiate markings is a conchoidal fracture lying outside the true area of the specimen, which is marked by dark colouration; there is no suggestion of pleural spines, rather the lateral profile is fairly straight; there is no hint of a telson. The

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specimen (MUGD 1201, not 1801 as quoted by Chapman, refigured here as Pl. 56, fig. 5) consists for the greater part of the thoracic area of a trilobite with relatively wide axis (13·5 mm) and narrow pleurae (6·3 mm). The pygidium is entirely missing and the fragmentary cephalon shows no detail at all. It is probably a poorly preserved homalonotid trilobite (pers. com. K. S. W. Campbell and P. A. Jell). One such species, *Trimerus harrisoni* (McCoy, 1876), has been described from the Dargile Formation in the Melbourne area. Chapman's damaged specimen has been compared alongside the holotype of *T. harrisoni*, NMV P7503. The axis of Chapman's specimen is more clearly demarcated than in the holotype of *T. harrisoni*, but the latter has suffered very little distortion compared with the former. The clearer delineation of the axis of '*H*' *tunnecliffei* is taken to be a result of the distortion. It is highly probable that the name *H. tunnecliffei* is a junior synonym of *Homalonotus harrisoni* McCoy (reassigned to *Trimerus* by Gill 1949).

SYSTEMATIC PALAEONTOLOGY

Repositories. The repositories of specimens quoted are denoted by the following abbreviations: MM, Geological and Mining Museum, Sydney; MUGD, Department of Geology, University of Melbourne; NMV, National Museum of Victoria, Melbourne.

Superfamily LIMULOIDEA Zittel, 1885

1885 Limulidae Zittel, p. 643.
1944 Limulacea Zittel; Raymond, p. 504.
1952 Limulacea Zittel; Størmer, p. 636.
1955 Limulacea Zittel; Størmer, p. P21.
1975 Limulacea Zittel; Bergström, p. 303.

Discussion. The suffix of the superfamilial name has been changed in conformity with Recommendation 29A of ICZN. Størmer (1952, 1955) included three families in the Limuloidea: Paleolimulidae Raymond, 1944; Mesolimulidae Stormer, 1952; and Limulidae Zittel, 1885. The family Limulidae was redefined by Riek and Gill (1971) to include those genera previously referred to the Mesolimulidae, thus comprising the genera *Limulus*, *Tachypleus*, *Carcinoscorpius*, *Mesolimulus*, *Psammolimulus*, and their new genus *Victalimulus*. They excluded the genus *Limulitella* Stormer, 1952, placing it with the Paleolimulidae and regarding it as a probable synonym of *Paleolimulus*. The type species of *Limulitella*, *Limulus bronni* Schimper, 1850, is in need of re-examination to establish the status of the genus. A fourth family name, Austrolimulidae, was established by Riek (1955) for the highly individual *Austrolimulus*; no other genus has yet been referred to this family. Vía Boada and Villalta (1966) established a new family Heterolimulidae for their genus *Heterolimulus* from the Triassic of Spain. Bergström (1975) summarized the classification up to this point. More recently Romero and Vía Boada (1977) described the genus *Tarracolimulus* from the same horizon as *Heterolimulus*, and included the latter without comment in the family Limulidae, a conclusion with which I agree.

Dubbolimulus gen. nov. has features which differentiate it from each family (although, if *Limulitella* is set aside because of its doubtful status, two of the families contain but a single genus), so that it would be possible to establish a separate family for it. *Dubbolimulus* can be separated from the Austolimulidae by the absence of exaggerated genal spines and of 'free posterior segments' on the opisthosoma. It is distinguished from the Paleolimulidae by the fact that the ophthalmic ridges do not meet in front of the cardiac lobe, by the absence of distinct annulation of the axis of the opisthosoma, and by the absence of movable lateral spines on the opisthosoma. This last feature represents a point of similarity with the Austrolimulidae; *Austrolimulus* is the only other limuloid genus which lacks movable spines on the opisthosoma. A characteristic peculiar to the Austrolimulidae is the fact that the anterior margin of the opisthosoma, at its junction with the prosoma, extends well beyond the area bounded by the ophthalmic lobes (Riek 1968*b*, fig. 1), whereas there is a clear correlation between these two features in other genera.

Features which distinguish *Dubbolimulus* from genera of the Limulidae are: (*a*) absence of movable spines, (*b*) apparent absence of free lobes on the anterior part of the opisthosoma, (*c*) the greatly unequal prosoma and opisthosoma, and (*d*) genal angles which are distant from the lateral margins of the opisthosoma. Setting aside (*c*) and (*d*) as being possibly of lesser significance phylogenetically, the other two characters could be either features which no antecedent of *Dubbolimulus* ever possessed, or ones which have been secondarily lost. Movable spines are unknown in Palaeozoic Limulina until the Permian *Paleolimulus avitus*, in which both the movable spines ('stylets') and the free lobe are specifically mentioned by both Dunbar (1923) and Raymond (1944). According to Ivanov (1933, fig. 54) the movable spines originate as the distal tips of the somites of the opisthosoma, which separate and move posteriorly during development of the embryo, being already present in the first larval stage. In view of the complexity of such a development it seems reasonable to regard all those forms in which it is expressed as belonging to a single lineage. The same applies to the sharing of somite VI, between the prosoma and opisthosoma, which appears to be connected with the production of the free lobes of the opisthosoma. These two features are fairly general among Limuloidea. Bergström (1975, p. 295) regards the sharing of somites VI and VII between prosoma and opisthosoma as distinctive of the suborder Limulina.

While the gross characters of *Dubbolimulus* link it to genera of Limulidae and Paleolimulidae, it is considered likely that the apparent absence of the free lobe on the opisthosoma is due rather to a masking of the characteristic by general simplification of morphological features of the opisthosoma, and that the absence of movable spines is another expression of the same trend. Phylogenetically, this means that *Dubbolimulus* is an offshoot of the main lineage of Limuloidea, rather than an independent derivative of a lineage closer to either Belinuroidea or Euproopoidea. This conclusion notwithstanding, *Dubbolimulus* cannot be assigned to either of the subfamilies of Limulidae, which are distinguished on the basis of characters entirely lacking in *D. peetae*. Although it shares the absence of movable spines with *Austrolimulus* and is of approximately the same age, the extraordinary genal spines and the 'free posterior segments' of the opisthosoma of *A. fletcheri* preclude consideration of any close relationship between *Austrolimulus* and *Dubbolimulus*. It is therefore appropriate to establish a new family for the latter. Raymond's original diagnosis of the superfamily (1944, p. 504) included movable lateral spines as a criterion. Their absence in *Dubbolimulus* and *Austrolimulus* excludes this as a suprafamilial character.

An alternative phylogeny for xiphosurans has been presented by Fisher (1981, 1982), based on cladistic principles. This focuses on the nature of the prosoma/opisthosoma articulation, and varies from earlier suggestions (e.g. Bergström 1975) in deriving the Limuloidea and Euproopoidea independently from the Belinuroidea. Both the younger groups are characterized by fusion of the opisthosomal segments, and Fisher uses the declination of the occipital band of the prosoma to determine polarity of various conditions of it with respect to the primitive (unfused) condition of the opisthosoma. Fisher (1977) has argued in favour of a ventral enrolment in *Euproops*, affording protection of the underparts. The articulation in *Limulus*, however, serves to achieve strong flexuring in the dorsal direction (Richter 1964), associated with righting strategies; the remarkable ophthalmic spines of *Euproops* absolutely preclude any similar dorsal flexuring, even had the structure of the occipital band allowed it. It seems to me that the morphological differences in the occipital band discussed by Fisher (1981) reflect these differences in function, which are in all probability generally characteristic of each superfamily.

The free segments reported at the rear of the opisthosoma in *Paleolimulus* (one segment) and *Austrolimulus* (three segments) support a derivation of Limuloidea from Belinuroidea. However, there appears to be some doubt about the nature of these structures. The most recent reconstruction of *Paleolimulus* by Fisher (1981, fig. 3B) excludes such a segment, and Raymond (1944, p. 50) seems to have had some reservation concerning it. I have examined the holotype of *A. fletcheri* with specific reference to this point. Certainly there are indistinct features suggesting transverse structures at the rear of the opisthosoma, but the 'segments' are definitely fused and were incapable of any independent movement. More significantly, they are confined to the area of the opisthosomal doublure, and thus had no appendages corresponding to them. Separation of the counterparts of the holotype has resulted in a transverse fracture of the exoskeleton anterior to these 'segments', so that the posteriormost part of the opisthosoma is held on the dorsal counterpart. Consequently, although only dorsal features can be observed for most of the skeleton, the rear of the opisthosoma and the telson can only be observed in ventral view. While the possibility remains that the poorly expressed transverse features represent true segmentation, the absence of any trace of appendages tends to belie such an interpretation. In the absence of material, other than the holotype specimen, with which to check this feature, it seems wiser not to regard the transverse structures as reflecting a true segmentation, and it should not be considered a primitive character in either *Paleolimulus* or *Austrolimulus*.

A comprehensive phylogeny of xiphosurans is presented by Fisher (1982, text-fig. 1). The nature of the text of his article implies that this phylogeny was arrived at by cladistic analysis. However, no discussion of the parameters used in achieving the result is presented, which makes it difficult to compare *Dubbolimulus* on the same basis. It is difficult to understand his close placement of *A. fletcheri* with *Psammolimulus gottingensis* and *Limulitella bronni*. *Austrolimulus*, with its reduced opisthosoma, exaggerated genal spines, absence of movable spines, and absence of posterolateral facets, is the most aberrant of all limuloids known so far; none of these features is characteristic of either of the other two genera on this branch of Fisher's proposed phylogeny. I regard both *Austrolimulus* and *Dubbolimulus* as being derived independently from the mainstream of Limuloidea.

Some of the remarks made by Fisher (1981) relating to the function of certain features of the limuloid carapace are of interest in the present context: in particular, (*a*) reduction of prosomal spines, reducing drag during swimming, (*b*) the significance of the free lobes in maintaining channels for respiratory currents during shallow burial, and (*c*) the function of movable spines as sensors against the substrate. All three of these features are reduced in both *Austrolimulus* and *Dubbolimulus* and, in the light of Fisher's observations, allow comment on the autecology of these genera. Fisher (1981, p. 57) predicts an association between development of free lobes and the importance of burrowing and burial in the activities of limuloids. This is an attractive suggestion which, coupled with the reduction in drag during swimming because of the absence of spines, suggests that swimming heavily outweighed burrowing in the relative significance of the activities of *Dubbolimulus*. Further support for this suggestion comes from Fisher's (1975) analysis of degree of vaulting of the prosoma in *Limulus* (strongly vaulted) and *Mesolimulus* (much flatter), in which he concludes that the two shapes are better suited to burrowing and swimming respectively. As the prosoma of *Dubbolimulus* was probably much flatter than that of *Limulus*, this strengthens the suggestion that burrowing was not an important activity of *D. peetae*.

The movable lateral spines, which occur in all limuloid genera except *Austrolimulus* and *Dubbolimulus*, serve to transmit information from the substrate, allowing precise orientation. The extended genal spines of *Austrolimulus*, coupled with the long telson, provide a refined mechanism of maintaining orientation (in both longitudinal and lateral senses) probably more critical than that provided by the movable spines; this could account for the obsolescence of movable spines in that genus. *Dubbolimulus*, however, does not show any features which could take over this function of the movable spines, so their absence in that genus remains unexplained.

Family DUBBOLIMULIDAE fam. nov.

Type genus. *Dubbolimulus* gen. nov.

Diagnosis. Limuloidea without dorsal or lateral spines, except for the genal angles of the prosoma and the posterolateral terminations of the opisthosoma adjacent to the telson joint; opisthosoma fused, much smaller than the prosoma; genal angles distant from lateral margins of opisthosoma.

Genus *Dubbolimulus* gen. nov.

Type species. *D. peetae* sp. nov.

Diagnosis. Prosoma semicircular, smooth; posterior margin lying near 90° to axis and bearing posteromarginal facet; opisthosoma with smoothly curved lateral margin without lateral spines;

scarcely wider than the distance between the ophthalmic ridges of the prosoma; free lobes not apparent on dorsal surface of opisthosoma.

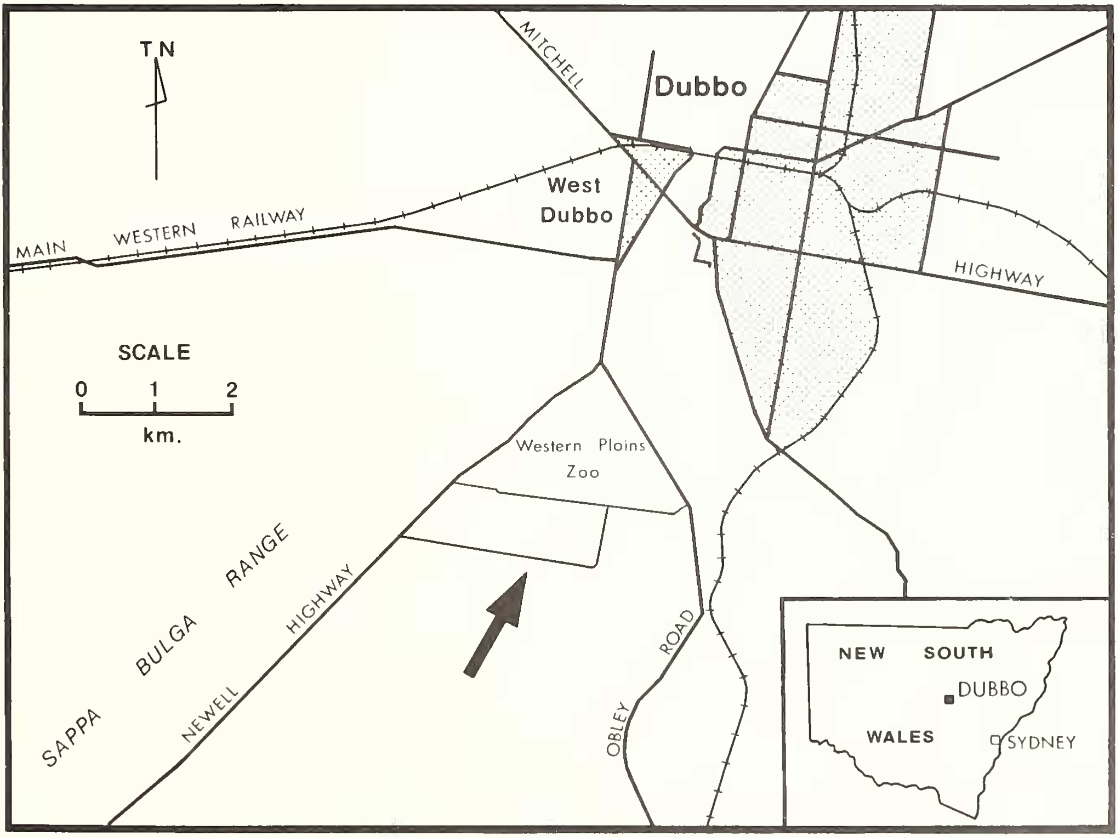
Derivation of name. From the type locality near Dubbo, New South Wales, Australia.

Dubbolimulus peetae sp. nov.

Plate 55; Plate 56, figs. 3, 4

Diagnosis. As for genus.

Material. Holotype and only specimen preserved as counterparts MM F27693 (dorsal) and MM F27694 (ventral). The specimen is preserved in a red-brown, iron-rich, slightly micaceous shale with common plant remains, most conspicuously *Dicroidium odontopteroides* var. *moltenense* Retallack. The specimen was recovered south of Western Plains Zoo, Dubbo, at approximate grid reference 151004 (yards), Dubbo 1:250,000 geological sheet (SI/55-4), 148° 37′ E, 32° 19′ S (text-fig. 1). Plant fossils are abundant at the locality, including many species illustrated in a recent paper by Holmes (1982) which deals with the flora of a locality 15 km to the south. This flora was considered middle Triassic by Holmes.



TEXT-FIG. 1. Map of the district around Dubbo, New South Wales, showing the type locality of *Dubbolimulus peetae* gen. et sp. nov. arrowed.

Description. The specimen consists of the flattened prosoma and opisthosoma, still in juxtaposition. The telson is lacking. Traces of some of the appendages have been impressed through the carapace. Separation has occurred in the dorsal exoskeleton, as there is little difference between dorsal and ventral counterparts (Pl. 55, figs. 1, 2); traces of the appendages are clearer in the ventral counterpart. The specimen may have been lying in a slight depression before burial, as compression has depressed the inner parts of the prosoma below both the prosomal margin and the opisthosoma.

The outline of the flattened prosoma approximates closely to a semicircle. It is 27·8 mm wide immediately in front of the genal angles and 14·0 mm long. The dorsal surface is marked by ophthalmic ridges which begin near the posterior margin at a point midway between axis and lateral margin. The compound eyes begin *c*. 1·0 mm anterior of this point, and are probably just under 2·0 mm long. The visual surface of the eye is not adequately preserved, but its position is marked by an outward inflection in the ophthalmic ridge. In front of the eye the ridge curves gently inward and runs forward again to a point 6·5 mm from the posterior margin and 5·5 mm from the axis, where it is inflected axially. The ophthalmic ridge is not continuous across the front of the prosoma, but terminates at a point 3·5 mm from the axis and 3·0 mm from the anterior margin. The left ophthalmic ridge is not as well preserved. The cardiac lobe is trapezoidal, 4·0 mm wide posteriorly, 2·3 mm wide at the front, and 7·0 mm long. The axial furrows are now the highest points on the flattened specimen, presumably corresponding to a greater amount of cuticular material beneath (apodemes, ventral exoskeleton, appendages). The axis is depressed and is marked by a crack (without separation) which reaches to within 3·0 mm of the anterior margin. It is not possible to count the number of apodemes, though there were certainly not less than four. The genal angles are produced into short (1·5 mm), blunt, genal spines which project posterolaterally. There may have been a narrow border (*c*. 0·2 mm wide) similar to that in *Limulus*, but details of this are obscured by flattening, possible concentric fracturing near the margin, and the fact that the doublure, apparently markedly angulated like that of *Limulus*, is impressed through the dorsal skeleton. The trace of this angulation disappears 3·0 mm from the posterior margin, suggesting that the angulation fades out, as in *Limulus*. In *Limulus* the angulation defines a triangular widening of the doublure in front of the mouth; this preoral area is present in *Dubbolimulus*, but is semicircular and clearly impressed through the carapace. There is a slight indication of a pair of median ocelli 7·0 mm from the anterior margin, where an increase in height of the ridge produced by the longitudinal axial crack suggests the original presence of a short, axially aligned, ocellar ridge. Alternatively, a median structure represented by an anteriorly convex curve 1·5 mm wide and 2·1 mm from the anterior margin may represent the trace of an ocellar tubercle forming the anterior edge of the interophthalmic region (Pl. 56, fig. 4, arrows). The posterior margin of the prosoma is rather straight, deflected posteriorly only at the genal angles. Between the posterior margin and the rounded anterior portion of the prosoma are triangular areas, here termed posteromarginal facets (after Meischner 1962, p. 185, 'hintere Randfacette'); they are defined by the inner edge of the genal spine, the posterior edge of the cardiac lobe, and the posterior end of the ophthalmic ridge. The anterior margins of the posteromarginal facets are formed by an angulation along which the dorsal surface of the prosoma is deflected ventrally. Crushing of the facets during compression has obscured details of morphology along most of the posterior margin of the prosoma.

The opisthosoma is conspicuously smaller than the prosoma, measuring 12·0 mm across its greatest width near the junction with the prosoma, and 7·5 mm from the anterior margin to the lobes on either side of the telson attachment; this makes it about equal in size to the area within the ophthalmic ridge of the prosoma. The lateral margins run parallel for 2·0 mm before turning axially, so that the opisthosoma tapers markedly to a minimum width of 4·2 mm, 1·5 mm from the posterior margin, which has a shallow re-entrant *c*. 1·0 mm deep for the telson attachment. The lateral margins bear no trace of either fixed or movable spines. As on the prosoma, the cardiac lobe is defined by the most raised part of the specimen, bounding a trapezoidal area 4·0 mm wide anteriorly and 2·5 mm wide at the rear. These ridges show traces of probably six apodemes. The area between the ridges is rather depressed. The lateral margins show a narrow border not more than 0·5 mm wide, which may correspond to the ventral doublure. If this is the case, the doublure is relatively narrower than in *Limulus*, possibly reflecting the absence of lateral spines. There is no indication of anterolateral free lobes on the opisthosoma; rather, the

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EXPLANATION OF PLATE 55

Figs. 1, 2. *Dubbolimulus peetae* gen. et sp. nov. Holotype specimen. Ballimore Formation, middle Triassic, Dubbo, New South Wales, ×4. 1, MM F27693, upper counterpart, showing the impression of the doublure, the posterolateral facets, and suggestions of apodemes on the opisthosoma. 2, MM F27694, lower counterpart, low angle lighting showing the appendages.

1

2

PICKETT, *Dubbolimulus*

doublure continues around the anterolateral corner, whereas in *Limulus*, with its well-developed free lobes, the morphology is quite complex in this area.

Some prosomal appendages have been impressed through the carapace (Pl. 55, fig. 2). Traces of five appendages are evident on the right side. Assuming that appendage I (the chelicera) would not be apparent and that the first ridge represents appendage II (by analogy with *Limulus*), a group of four legs (appendages II–V) is succeeded by a gap (in which there are two smaller, unidentified impressions) and another long, laterally directed leg, corresponding to the posteriorly directed appendage VI of *Limulus*. None of the legs projects beyond the rim of the carapace, but legs V and VI almost reach it. No joints in the legs are discernible. They are almost straight, with a slight anterior curve. On the left there are less regular impressions of possibly five legs reaching almost to the margin, but except for appendage VI these are less easily identifiable.

A possible reconstruction of *D. peetae* gen. et sp. nov. is shown in text-fig. 2.

Discussion. The specimen has been much flattened during compaction of the sediment. This is most obviously expressed as (*a*) the impression of legs, doublure, and apodemes through the carapace, (*b*) the presence of an axial crack and some damage in the region of the left ophthalmic ridge, and (*c*) wrinkles on the outer part of the prosoma. This latter point particularly may reflect the fact that the exoskeleton was not strongly mineralized. The wide angle between the rear margin of the prosoma and the lateral edges of the opisthosoma is an unusual feature in limuloids, and was originally attributed to anterolateral movement of the genal angles during compaction.

To examine the effects of compression on limuloids, four juvenile specimens of *Limulus polyphemus* were embedded in clay and subjected to considerable pressure applied by means of screw clamps. Some lateral spread occurred in all cases, the least amount occurring in the specimen illustrated in Pl. 56, fig. 1, in which the maximum width of the prosoma increased by 1·4%. The length of the prosoma, however, was *reduced* by over 10%. In no case was there any change which suggested that the condition observed in *Dubbolimulus* could have resulted from the spreading of an original configuration of genal angles similar to that in *Limulus*. The prosoma outside the ophthalmic ridges has suffered the greatest damage, being compressed into a number of concertina-like folds roughly concentric with the margin. It is apparent that the dorsal spines greatly reinforce the exoskeleton (thicker at these points), as the areas around them have suffered little crushing. Probably for this reason there is no development of a longitudinal axial crack as in the holotype of *D. peetae*, since young *L. polyphemus* have six axial spines, three on the prosoma and three on the opisthosoma. Insufficient pressure was achieved to impress the appendages through the dorsal exoskeleton. By contrast, a specimen flattened between numerous sheets of paper in a hydraulic press suffered considerable anterolateral movement of the genal angles, and the spines on the ophthalmic ridges were flattened sideways.

EXPLANATION OF PLATE 56

Fig. 1. *Limulus polyphemus*. Epoxy resin cast of juvenile specimen compressed in deformation experiment. Note the concentric folds of the exoskeleton outside the ophthalmic ridges, and the proximity of the genal spines to the lateral margins of the opisthosoma, ×0·95.

Fig. 2. *Pincombella belmontensis* Chapman. NMV P13646, latex cast of holotype, Boolaroo Sub-group, late Permian, Belmont, New South Wales, ×7·5.

Figs. 3, 4. *Dubbolimulus peetae* gen. et sp. nov. MM F27693, holotype, Ballimore Formation, middle Triassic, Dubbo, New South Wales. 3, upper counterpart, ×1. 4, detail of upper counterpart showing median area of prosoma in ocellar region, ×14; the arcuate structure is the rear edge of the doublure; arrows indicate the levels of structures which may be interpreted as ocelli.

Fig. 5. *Trimerus harrisoni* (McCoy). MUGD 1201, latex cast of '*Hemiaspis*' *tunnecliffei* Chapman, Dargile Formation, late Silurian, Studley Park, Melbourne, Victoria. The area in shadow near the top of the figure lies outside the real margin of the specimen, but is what was interpreted as a wide border with radiate markings by Chapman (1932, pl. 14, fig. 5). Thoracic pleurae are visible on the right, but only the posterior pleurae are preserved on the left, ×1.

PLATE 56


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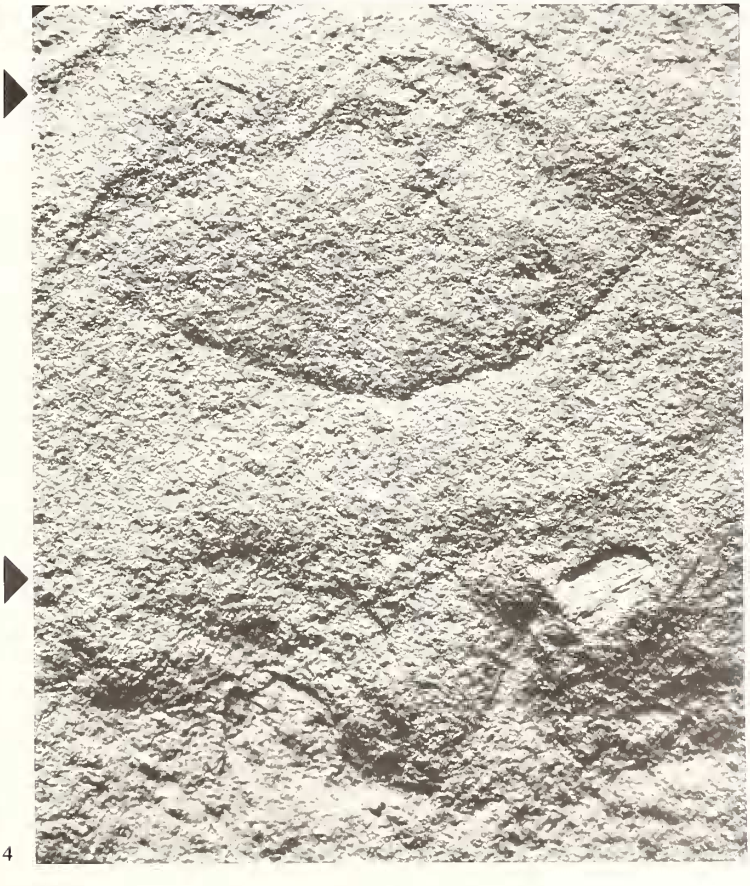
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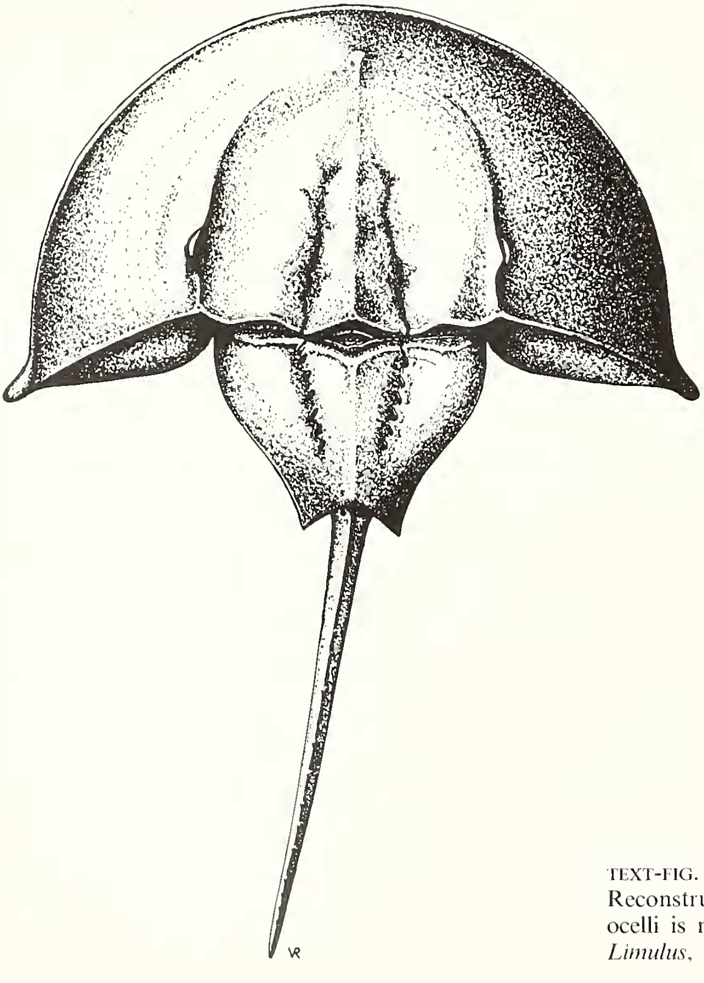
It is apparent that the hydraulic conditions of compression under geological circumstances hinder lateral spreading of strongly profiled organisms, as established by Walton (1936) and Rex and Chaloner (1983) for plant compressions. I thus conclude that the outline of *Dubbolimulus* as preserved is very close to the original. Having determined this, there is some support for the undisturbed rear margin of the prosoma from other aspects of the morphology. If the prosoma was moderately arched (as it must have been to create room for the appendages, their musculature and the digestive organs), the possibility emerges, with an outline like that of *Dubbolimulus*, that the arched posterior margins beyond the edges of the opisthosoma left a wide gape, exposing the underparts of the prosoma. Such a morphology would be out of character with the general style of limuloids, which are close to their substrate on all sides so that their ventral surface is well protected. The rear margin of the prosoma of *Dubbolimulus* bears a triangular area on either side of the interophthalmic region which is interpreted as a ventrally deflected posteromarginal facet, thus largely closing the gape at the rear of the prosoma. This structure occurs in *Psammolimulus* (Meischner, 1962) and *Victalimulus*, though not described in the latter. It is also present in the oldest member of the group, *Paleolimulus*, being clearly indicated in Dunbar's (1923) figures, in '*Limulus*' *woodwardi* Watson, 1909, and in *Mesolimulus walchi*, in which it has a somewhat exaggerated development.



TEXT-FIG. 2. *Dubbolimulus peetae* gen. et sp. nov. Reconstruction by Vivien Reid. The position of the ocelli is not certain, and the telson is based on *Limulus*, ×3.

Ivanov (1933, fig. 63) figured a specimen of *M. walchi* and remarked (1933, p. 295) that, on the underside of the prosoma, there is an obvious furrow corresponding to the pleural part of the anterior border of the sixth segment. He equated this with a ridge in the same position on the dorsal surface of other specimens. This structure may be one taken up by Stormer as a primitive feature (1952, p. 630: 'A furrow along the inner margin of the genal angles may also be a primitive character'). It is possible that the angulation at the anterior border of the posteromarginal facet corresponds to the boundary between segments V and VI but, as it appears to have a function in protecting the ventral surface of the prosoma, this is not necessarily so.

Habitat. Dubbolimulus was recovered from strata which are undoubtedly of freshwater origin. No marine Triassic rocks are known in New South Wales, the nearest being 800 km distant near Gympie in Queensland (Fleming 1966; Runnegar 1969). The Ballimore Formation is the basal unit of the Great Artesian Basin in the Dubbo area, and lies unconformably on folded strata of Ordovician to Devonian age. The oldest marine strata in the New South Wales portion of the Great Artesian Basin are early Cretaceous (Aptian) in age (Scheibnerová 1976; Morgan 1980); the marine succession in this basin is the result of a north to south transgression. To the east there was an area of high land, just as there is today. Thus the locality was probably as remote from the ocean in Triassic times as it is at present, and any possibility of marine influence can be ruled out. The general area abounds in plant fossils (e.g. Holmes 1982), indicating a limnic situation, and the specimen of *Dubbolimulus* was recovered while collecting plant fossils. Riek and Gill (1971) suggested that their specimen of *Victalimulus*, also from freshwater strata, may have migrated there for breeding purposes. In view of the distance of the type locality from any areas of marine sedimentation, such a possibility seems remote for *Dubbolimulus*.

There has been a certain reluctance on the part of palaeontologists to attribute a freshwater habitat to fossil limuloids (Riek and Gill 1971; Holland *et al.* 1975). None the less, in addition to the species described by those authors (*V. mcqueeni* and *Casterolimulus kletti*), there are others which have been recovered from non-marine strata: *A. fletcheri* (Riek, 1955), *Psammolimulus gottingensis* (Meischner, 1962). On the other hand, species of undoubted marine origin are *M. walchi* (Størmer 1952; Barthel 1974), *Heterolimulus gadeai* and *Tarracolimulus rieki* (Vía Boada *et al.* 1977), '*Limulus*' *woodwardi* (Watson, 1909) and '*L.*' *syriacus* (Woodward, 1879). Species referred to *Limulitella* appear to belong to both groups, e.g. *L. bronni* (Bill, 1914) and *L. liasokeuperinus* (Braun, 1860) appear to be from non-marine strata, whereas *L. vicensis* (Bleicher, 1897) is marine.

Colleagues have been strongly influenced by the marine nature of modern limulids, and by the rare reports of some species in fresh waters. However, Annandale (1909, p. 295) claimed that *Carcinoscorpius rotundicauda* is 'mainly if not entirely estuarine' and indicated that it occurs almost 150 km from the mouth of the Hooghly River. The remoteness of *Dubbolimulus* from any marine areas suggests strongly that its whole life cycle was spent in fresh water. Riek and Gill (1971, p. 207) have suggested that *Victalimulus* migrated to fresh water for breeding. If one accepts a migration between marine and limnic environments for *V. mcqueeni*, it seems more likely, in view of the basically marine nature of extant forms, that the breeding phase would have been marine, as, for instance, in many Recent terrestrial crabs.

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